TRANSPIRATION AND CO_2 FIXATION OF SELECTED DESERT SHRUBS AS RELATED TO SOIL-WATER POTENTIAL

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ABSTRACT.— In desert plants, transpiration rates decreased before photosynthetic rates when plants were entering a period of water stress. This may have adaptive consequences. A difference of –5 bars in the soil-moisture potential had considerable importance in reducing the rate of transpiration. In *Helianthus annuus* L. (sunflower) the photosynthetic rate decreased before the transpiration rate in contrast to Great Basin-Mojave Desert plants, and the changes occurred with a –1 bar difference in soil-moisture potential. Morphological changes in three desert plant species [*Artemisia tridentata* Nutt., *Ambrosia dumosa* (Gray) Payne, *Larrea tridentata* (Ses. Moc. ex DC) Cov.] as the soil-moisture potential decreased are given. With a mesic species, *H. annuus*, 20 percent reduction in photosynthesis and transpiration was reached at higher soil-moisture potentials than with the desert plants. Loss of net photosynthesis occurred in *A. dumosa* (a summer deciduous shrub) as Ψsoil reached –48 bars in the field, whereas *L. tridentata* (an evergreen shrub) at the same time was able to maintain a water potential difference betwen soil and plant of –10 to –15 bars and continue net CO_2 gain well into the summer months.

Plants growing in arid regions obviously have the capability of surviving conditions of low soil-water content. The mechanisms differ (Cooper 1975). Transpiration and photosynthesis are two important plant processes that must adapt to the dry conditions for survival. Both processes involve gas exchange between the plant and the atmosphere, and both are known to decrease as soils become drier or as moisture stress increases (Babalola et al. 1968, Cox and Boersma 1967, El-Rahman 1969, Fischer 1970, Heichel and Musgrave 1966, Pallas et al. 1967, Schneider and Childers 1941, Schratz 1937, Shinn and Lemon 1968). Obviously, plants which have very low transpiration rates, thus prolonging the water supply provided that leaf turgor remains in a satisfactory state, would be favored under arid conditions. Also, a relatively high rate of photosynthesis could be advantageous, especially if it could be maintained with decreasing transpiration rates due to drying of soil.

Studies of quantitative relationships among transpiration, photosynthesis, and soil-water potential for desert shrubs have generally been difficult in the past because of technical difficulties. Desert shrubs grow and survive under conditions where the soil-water potential is usually much lower than can be accurately monitored by soil-water potential monitoring devices such as tensiometers or resistance blocks. However, recent developments of thermocouple psychrometers for measuring water potential extended the range that can be measured in soil. More sophisticated instruments that measure water vapor and CO_2 exchange between plants and the surrounding atmosphere have also been developed (Koller 1970, Mork et al. 1972). In particular, a null-point system that maintains a given atmospheric condition is desirable because the exchange is not greatly influenced by the measuring technique (Koller 1970, Mork et al. 1972).

The purpose of the research reported herein was to measure the relationship between transpiration and photosynthesis and soil-water potential of various desert shrubs. One study was conducted on sunflowers to provide comparison with a plant not adapted to desert conditions.

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MATERIALS AND METHODS

Studies were conducted under glasshouse conditions in containers so that the soil-water condition throughout the root zone could be determined. The plant species studied were *Artemisia tridentata* Nutt., *Ambrosia dumosa* (Gray) Payne, *Larrea tridentata* Ses. Moc., and *Helianthus annuus* L. (sunflower).

Rooted cuttings of *A. tridentata* (Wieland et al. 1971), along with seedlings of the other plant species, were grown in either 900 ml (10.5 cm diameter and 15 cm deep) or 2700 ml (10.5 cm diameter and 45 cm deep) containers. A Yolo silt loam soil treated with "krilium" to maintain aggregate stability was used as a growth medium. All containers were watered to approximately 20 percent soil-water content (Ψ soil = –1) and maintained until roots were established throughout the container. After roots were fully established, some of the containers were watered on a regular basis, whereas others were allowed to dry out.

Soil-water potential (Ψ soil) was measured by thermocouple psychrometers. (Commercial psychrometers manufactured by Wescor Inc., Logan, Utah were used. Readout was on a Keithley Nanovoltmeter.) One psychrometer was placed at 10 cm depth in the 900 ml container, and three psychometers were placed at 10, 28, and 42 cm depths in the 2700 ml containers.

Soil-water potential measurements were made early in the morning after plants were taken from the greenhouse into the headhouse to prevent rapid increase in soil temperature that interferes with potential measurement. Plants were allowed to stand in the headhouse for approximately one-half hour before measuring the potential, and then the containers were returned to the greenhouse.

Transpiration and apparent photosynthesis were monitored on both watered and unwatered plants. These measurements were made by a null-point compensating system described by Koller (1970) and further modified by Mork et al. (1972). Briefly, the measuring procedure was as follows: The plant was enclosed in a chamber that was maintained at constant relative humidity, temperature, and carbon dioxide concentrations. The amount of water removed to maintain constant relative humidity was measured and represented the transpirational loss from the plant. The amount of CO_2 added to the chamber to maintain the constant concentration was also measured and represented apparent photosynthesis. The plant chamber was used in the greenhouse; thus light intensity was not maintained constant and represented an uncontrolled variable. Light intensity measurements were made and recorded for the time transpiration, and apparent photosynthesis measurements were made. The plant chamber was maintained at a relative humidity of 28 percent, a CO_2 concentration of 316 μl/liter and a temperature of 25 C.

The time required for the plant to remain in the chamber depended upon the rate of transpiration and apparent photosynthesis. Sufficient water and CO_2 had to be exchanged for significant results. A 20-minute period generally was sufficient when transpiration and apparent photosynthesis were quite rapid, as occurred for nonstressed plants. Monitoring periods of up to an hour were often required for the stressed plants because of the low transpiration and apparent photosynthesis of these plants.

Because of the time involved in making measurements, not many plants could be measured. Because both transpiration and apparent photosynthesis are dependent upon light intensity, day to day variations in light intensity were partially compensated for by reporting only points where major changes occurred. Representative data, however, are shown in Figure 1.

Artemisia tridentata plants were grown in both 900 ml and 2700 ml containers. Apparent photosynthesis and transpiration were measured over two drying cycles. *Larrea tridentata* plants were grown in 2700 ml containers, and the transpiration and apparent photosynthesis were monitored for one drying cycle on two plants. The *A. dumosa* and *H. annuus* plants were grown in 900 ml containers and monitored for one drying cycle.

Gas exchange measurements were made on *L. tridentata* and *A. dumosa* during the months of May and June in the Mojave Desert. Soil-water potential and plant-water potential were monitored simultaneously. The latter was monitored by the pressure

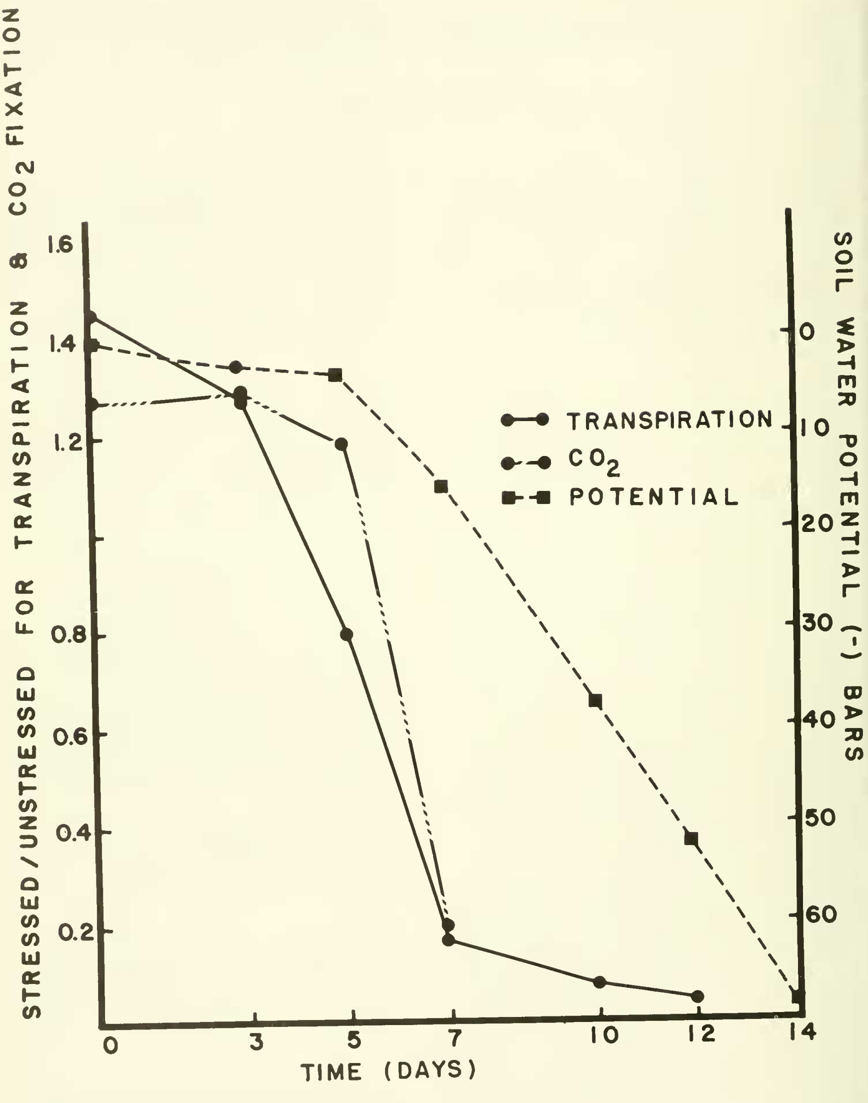

Fig. 1. Representative plot of data obtained, in this case for *A. dumosa*. Data are plotted as a ratio of stressed to unstressed plant conditions. Part of the variation in the ratio for zero time is due to differences in individual plants. Light intensity in 1000s μ Einsteins m^{-2} sec^{-1} in stressed plants for 0, 3, 5, 7, 10, 12, and 14 days, respectively, were 0.4, 1.4, 1.5, 1.2, 1.5, and 1.5, respectively. For unstressed plants for the same number of days they were 0.4, 1.2, 1.6, 1.1, 0.5, 1.3, and 1.5, respectively.

bomb technique (Scholander et al. 1965). Conditions for measuring photosynthesis and transpiration were the same as for greenhouse experiments.

RESULTS AND DISCUSSION

The results for *A. tridentata* are described in Table 1. At the beginning of the measurement, plants were in a vigorous state of vegetative growth; the stems were green and supple, the leaves were approximately 3 cm long, and the internodes approximately 0.5 cm apart. A shoot approximately ½ to 1 cm long was developing at each node. The lobes of the trees were deeply cleft, and the color was green with a slight shade of gray both on the upper and lower surfaces.

First visual indication of water stress on the plant was a gradual yellowing of the leaves attached to the main stem. As soil-water potential decreased over an 11-day period, the leaves turned necrotic and eventually fell off. The earlier symptoms occurred at a Ψ soil of –15 to –20 bars. A sharp reduction in transpiration and CO_2 fixation occurred when the soil was –5 to –10 bars. When the soil was between –20 and –25 bars, the remaining leaves wilted, and the overall color became more gray than green. No measurements on transpiration or apparent photosynthesis were made when Ψ soil was –25 bars; therefore, the plant in the dried soil was rewatered to start a second cycle.

Although the specific plant under test was not carried beyond –25 bars Ψ soil before watering, other plants were carried to lower potentials. The symptoms which occurred were that the shoot tips wilted and, if kept under stress, eventually died. However, the tips can be killed and the plant can recover if it is not held under stress too long.

Having the study plant subjected to 11 days without addition of water caused a noticeable change in plant appearance and characteristics even after irrigation. The stems were woody; internodes were quite close, giving the appearance of a whorl or rosette rather than single leaves alternately spaced as on the first cycle. The longer leaves were still attached, but were either yellow or necrotic.

There was an increase in the relative transpiration and CO_2 fixation rate following irrigation. The transpiration was initially high relative to the CO_2 fixation during the recovery period; however, the CO_2 fixation rate eventually was higher than transpiration. Upon starting the second drying cycle, decrease in transpiration appeared at a higher Ψ soil than did a decrease in CO_2 fixation. There was a steady decrease in transpiration as the Ψ soil decreased below about –2.5 bars. On the other hand, there appeared to be little effect of Ψ soil on CO_2 fixation until the soil-water potential was lower than about –16 bars. Further decrease in Ψ soil caused a decrease in CO_2 fixation. Within limits, a more rapid decrease in transpiration than decrease in CO_2 fixation as Ψ soil decreases may be an important factor in survival of plants adapted to arid environments. The

TABLE 1. Soil-moisture potential at which various changes occurred in the plants (–bars).

	H. annuus	*A. dumosa*	*L. tridentata* Plant No. 1	*L. tridentata* Plant No. 2	*A. tridentata*
20 percent reduction of photosynthesis rate	1	6	20	16	15
20 percent reduction of transpiration rate	2.5	3.5	5	26	5
Stress at CO_2 reduction of 75 percent	6	13	40	30	30
Stress at minimum CO_2 exchange	17	38	62	54	52

plant can be conserving water while still effectively producing carbohydrates. A recent review by Fischer and Turner (1978) on productivity in arid and semiarid environments suggests that plants tend to maintain high gas exchange rates as long as possible, thus maximizing both photosynthesis and transpiration.

Following are visual descriptions of the stressed plant as the Ψ soil decreased after the second irrigation. There were no visible symptoms of stress until Ψ soil was about –22 bars. This observation related quite closely to the CO_2 fixation but not to transpiration, as there had been a curtailment of transpiration well before visible symptoms occurred. The changes noted in the plant at –22 bars were an inward curling of the outer edge of the leaves; added stress induced by Ψ soil of –27 bars caused a very slight wilting. The change in plant appearance at –32 bars was a pronounced wilting and leaf color change from greenish to gray. When Ψ soil reached –52 bars, no apparent photosynthesis was measurable. Leaf tips became darker in color and severely curled. Soil-water potentials lower than about –61 bars were not measurable by the psychrometers in use (psychrometers more recently developed can measure below –61 bars). Thus, further observations on the plant refer to number of days following the time Ψ soil reached –61 bars.

After 5 days, the plant was under very severe stress, but there were no signs of necrosis except on leaves that had been damaged during the previous irrigation cycle. The method for measuring apparent photosynthesis was to monitor the amount of CO_2 required to maintain a constant CO_2 content in the plant chamber. Because there was no net CO_2 use at this high stress, the CO_2 concentration in the chamber was monitored with no air flow. With this change, the CO_2 concentration increased slightly and covering the chamber caused a threefold increase in rate of CO_2 production, indicating that some photosynthesis occurred at this time, even though it was not equal to the rate of respiration.

Seven days following the –61 bar potential readings, visible symptoms were about the same. CO_2 did increase slightly in the chamber, indicating respiration; however, the rate of CO_2 production did not change when the chamber was covered to eliminate light, thus indicating that photosynthesis had completely ceased.

Necrosis started to appear on lobes and margins of the leaves nine days following the –61 bar stress. Twelve days following the –61 bar Ψ soil reading the plant had a dull slate-gray appearance, the lower leaves were generally necrotic, and the upper leaves were flaccid. There was no change in CO_2 concentration within the chamber, indicating respiration had ceased. The plant was then irrigated, but it did not recover. It appears, therefore, that the plant can recover following irrigation at any time that measurable metabolism such as respiration can be found. Apparently, after the plant reaches a stage in which respiration completely ceases, it is irreversibly damaged.

In general, there were similarities between the results observed for plants grown in the 2700 ml container as compared to the 900 ml container even though the drying times to achieve the same level of stress were different. Transpiration decreased at a higher Ψ soil than did apparent photosynthesis during both the first and second irrigation cycles. However, during the second irrigation cycle, more time was required for the plant to recover in both photosynthesis and transpiration after having been subjected to water stress. The increase in apparent photosynthesis and transpiration following irrigation cannot be attributed completely to an increase in plant size because of growth. Although the drying period extended over a longer period of time in the 2700 ml container, the visual symptoms of the plant were very similar to those reported for the 900 ml container. During the first drying cycle, the longer leaves on the main stem curled and turned yellow. As drying continued, the other leaves changed to a grayer color with some curling. During the second drying cycle, there was no great appearance of chlorosis or necrosis of the leaves, but the leaves became a dull color and rolled.

The results for *A. dumosa* are also summarized in Table 1. This plant was carried over one drying cycle only. As was observed with *A. tridentata*, the transpiration appeared to decrease at a higher Ψ soil as compared to

CO_2 fixation. Transpiration noticeably decreased at Ψ soil less than –5 bars. A marked decrease in CO_2 fixation occurred when Ψ soil decreased from about –4 bars to about –15 bars. Apparent photosynthesis had ceased when the Ψ soil was –38 bars, however; CO_2 production was enhanced by covering the chamber, indicating that some photosynthesis was occurring at that Ψ soil even though respiration was at a higher rate than photosynthesis.

Some of the visual symptoms of *A. dumosa* are as follows: plants showed no symptoms of wilt, but the leaves were grayer than the control at a Ψ soil of –15 bars. As with *A. tridentata*, decrease in metabolic processes such as transpiration and photosynthesis occurred before visual symptoms appeared. Severe chlorosis on all but the leaves toward the growing tip occurred when the Ψ soil reached –38 bars. At this point there was no apparent photosynthesis, although some transpiration was still occurring. When the Ψ soil was –60 bars, the foliage was completely necrotic except for some color in the axils of leaves. This plant recovered if watered at this stage.

Soil in the containers of two separate *L. tridentata* plants was allowed to dry out. The *L. tridentata* plants were grown from seed and there was large variation between individual plants. One plant will be referred to as *Larrea 1*. Similar to other species, transpiration tended to decrease at a higher Ψ soil than did CO_2 fixation. However, the other plant (referred to as *Larrea 2*) showed an opposite trend that CO_2 fixation decreased at a higher Ψ soil than did transpiration. Differences between the two individual plants, however, go beyond these observations. The *Larrea 1* plant responded to drying out by having 50 to 60 percent of the leaves on the plant turn yellow and fall off when the Ψ soil was approximately –20 bars. The trend toward defoliation and yellowing of leaves continued as the water potential decreased. On the other hand, the *Larrea 2* plant had very little yellowing and defoliation under stress. Leaves tended to wilt and turn to a gray-green color. With continued soil drying, the leaves became desiccated. Some yellowing of leaves did occur, but the plant appeared completely different from the *Larrea 1* plant.

Results for the *H. annuus* plant are also in Table 1. One noticeable difference between *H. annuus* and the desert shrubs was that a slight decrease in Ψ soil down to –1 bar greatly reduced CO_2 fixation and did not have any significant effect on transpiration. Most of the desert shrubs behaved quite oppositely where transpiration was reduced much more significantly than CO_2 fixation at low soil. This may be of competitive advantage for the desert species. It has been reported that halophytes have lower transpiration rates than nonhalophytes (Schratz 1937), and this may be true also of other plants growing in harsh environments. A Ψ soil of –6 bars caused a great reduction in both transpiration and CO_2 fixation in *H. annuus* plant, but neither process could be monitored at a soil-water potential of –24 bars. When the Ψ soil reached –6 bars, the lower leaves were severely wilted and other leaves moderately wilted. When Ψ soil reached –20 bars, all leaves were severely wilted and the lower leaves complete necrotic. At Ψ soil of –33 bars the stem was shriveling.

The *H. annuus* experiment was conducted as an indicator of our procedure. Many studies have been conducted on drying soil in which *H. annuus* plants are growing, and –15 bars has often been quoted as the permanent wilting percentage for *H. annuus*; our results are in reasonable agreement with that value. Transpiration and photosynthesis measured on *H. annuus* also appear to be reasonable. This provides some degree of confidence in accepting the results measured on the desert shrubs.

The results of a field experiment where both soil-water potential and tissue-water potential (Ψ plant) (Scholander et al. 1965) were measured are shown in Table 2. Gas exchange measurements on *A. dumosa* during May and June showed decreasing photosynthesis and transpiration rates as Ψ soil decreased. Positive carbon dioxide exchange ceased on *A. dumosa* as Ψ plant reached –47 bars. However, *L. tridentata*, an evergreen desert shrub, continued photosynthesis until Ψ plant reached –65 bars. This difference between species is in agreement with greenhouse studies reported in Table 1 and also with results of Odening et al. (1974). *Larrea tridentata* has a distinct advantage of being

TABLE 2. Ψ soil and Ψ plant (–bars) as measured on two desert shrubs under field conditions.[*]

		Ambrosia dumoa		*Larrea tridentata*	
		Ψsoil	Ψplant	Ψsoil	Ψplant
May	1	22	39	22	51
	9	28	40	28	54
	31	42	—	42	56
June	1	48	47	48	63
	6	48	dormant	48	—
	12	50	dormant	50	63
	12	52	dormant	52	65

[*] Maximum rates of gas exchange for *A. dumosa* and *L. tridentata* were net photosynthesis 35 and 10 mg/g dry wt -h and transpiration 45 and 13 g/dry wt -h, respectively.

able to maintain productivity well into the summer months. In both shrub species, maximum gas exchange activity occurred during the early spring months when favorable moisture conditions existed.

ACKNOWLEDGMENTS

This study was supported by Contract EY-76-C-03-0012 between the U.S. Department of Energy and the University of California.

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